

Phylogeny of Genus *Scutigera* (Amphibia: Megophryidae): A Re-evaluation

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Abstract. - A re-analysis of a published data set from Ye et al. (1992) indicates that their phylogeny for the genus *Scutigera* does not reflect the most parsimonious explanation of the data. The consensus of the resulting trees from the original data set is a "bush" with only three resolved nodes. A re-evaluation of the character states, and their respective polarizations, resulted in alternative phylogenetic hypotheses. However, measures of homoplasy and data consistency for the re-evaluated topologies were relatively low, suggesting that little confidence could be obtained in these relationships. More data are needed to generate a defensible hypothesis of the relationships within the genus *Scutigera*.

Key words: Amphibia, Anura, Pelobatoidea, Megophryidae, *Scutigera*, morphology, phylogeny, parsimony

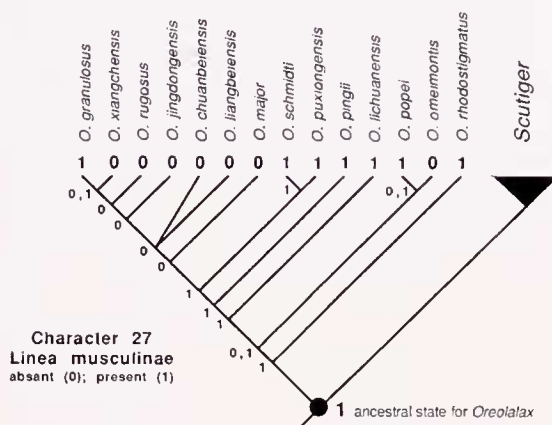


Figure 1. Phylogeny of *Oreolalax* with the character states of linea musculinae optimized on the tree. The primitive condition of linea musculinae for the phylogeny of *Scutigera* is 1.

Introduction

Frogs in the family Megophryidae have long captivated many herpetologists, especially Chinese colleagues, partly because of their supposed transitional position between "primitive" and "advanced" frogs (Lynch, 1973, Ford and Cannatella, 1992) and also because of aesthetic appeal. The phylogeny of pelobatoids is largely unknown, and we now realize that the concepts of "primitive" and "advanced" taxa are phylogenetically flawed and hence unacceptable; only character states have these attributes.

Thirty-two species of *Scutigera* occur in the high altitudes of the Tibet Plateau in southwestern China, Burma, Nepal, and northern India. A phylogeny of

this group has been wanting. The genealogical relationships of this group would be useful for assessing theories of the geologic events that have been linked with the uplift of this region. Recently, Fei and Ye (1990) and Xu et al. (1992) investigated the relationships of megophryids. Of particular interest, Ye et al. (1992) presented a phylogeny of genus *Scutigera* using 29 morphological characters. Unfortunately, some invalid methods were employed in both the character analysis and tree selection, and these nullify their hypothesis. We performed a re-evaluation of the Ye et al. (1992) data, and examined their proposed phylogeny of *Scutigera*.

Methods

The data of Ye et al. (1992) consisted of 29 morphological characters for 16 species of *Scutigera*, and one outgroup taxon (Appendix I). Initially, we analyzed these data without modification. Following Ye et al. (1992), five species, *Scutigera ningshanensis*, *S. maculatus*, *S. nepalensis*, *S. occidentalis*, and *S. adungensis*, were excluded from the analysis owing to many unknown character states (Appendix II). We used outgroup analysis (Maddison et al., 1984) to reassess character state polarizations. *Oreolalax* was used as the outgroup and polarizations of the character states were determined from previous work (Fu and Murphy, in press). From this phylogeny, we were able to identify pleisomorphic character states for *Oreolalax*, which were then used to polarize the character states for scutigerae. For example following Maddison et al. (1984) and Wiley et al. (1991), we assigned character states for the terminal branches down the tree until reaching the root node (see Fig. 1 for the optimization of Linea Musculinae).

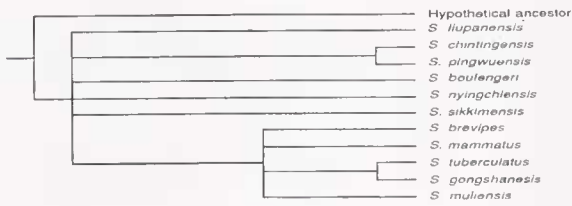


Figure 2. Strict consensus tree of the phylogeny of *Scutigera*, derived from our reanalysis of Ye et al.'s (1992) original data.

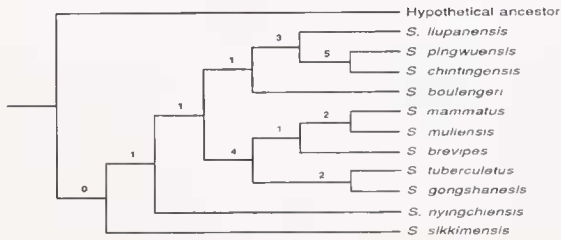


Figure 3. One of 20 MPTs depicting the phylogeny of *Scutigera* that was derived from our reanalysis of Ye et al.'s (1992) original data. When the outgroup condition was not known, the original character state polarizations of Ye et al. were used. This topology was reached by successive approximations (Farris, 1969); numbers indicate unambiguous synapomorphies occurring at each corresponding node.

Phylogenetic analyses were conducted using (PAUP) version 3.1.1 (Swofford, 1993) and employing an heuristic search with stepwise addition. Tree optimization was performed using the tree bisection-reconnection branch swapping option, steepest descent, and retaining all most parsimonious trees. Tree topologies were analyzed in MacClade 3.04 (Maddison and Maddison, 1992). To choose among the most parsimonious trees, we employed successive approximations (Farris, 1969). Decay analysis (Bremer, 1988) was used to assess nodal stability.

Results

Our initial evaluation of the phylogeny of *Scutigera* using the unmodified original data of Ye et al. (1992) resulted in 20 most parsimonious trees (MPTs), each with a consistency index (ci) of 0.46, retention index (ri) of 0.53 and a length of 62 steps. A strict consensus tree revealed only three consistent nodes (Fig. 2). *Scutigera gongshanensis* with *S. tuberculatus* were resolved as sister species, as were *S. pingwuensis* and *S. chintingensis*. Only the latter relationship and the association of *S. mammatus*, *S. brevipes*, *S. muliensis*,

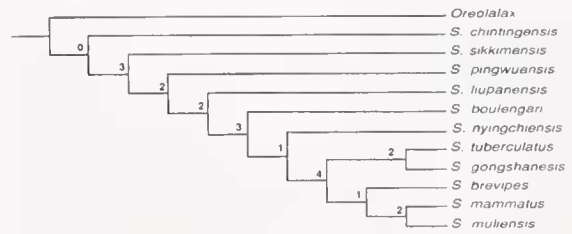


Figure 4. Phylogeny of *Scutigera*. One of 16 MPTs derived from Ye et al.'s (1992) data using *Oreolalax* as the outgroup. When the outgroup condition was not known, the original character state polarizations of Ye et al. were used. This topology was reached by successive approximations; numbers indicate unambiguous synapomorphies occurring at each corresponding node.

S. tuberculatus and *S. gongshanensis* were resolved by Ye et al. (1992). Excluding these relationships, all others were ambiguous. The topology of Ye et al. requires 63 steps to explain the data, one step longer than our most parsimonious tree. A successive approximations evaluation resolved a single tree, one of the original 20 MPTs (Fig. 3).

Re-examination of the character polarizations of Ye et al. (1992) shows that characters 3 and 27 were incorrectly polarized in the original work. We were unable to polarize character 25 because both states occur in the outgroup; the presence or absence of spinal patches on the forelimbs are equally probable as a plesiomorphy for *Scutigera*. Characters 1 and 26 have autapomorphic states only, making them phylogenetically uninformative; they were excluded from subsequent analyses. Polarization of characters 7, 8, 9, 10, 11, 15, and 17 was not possible using outgroup criterion because the state(s) in the outgroup are not known. These characters were treated both using the original polarizations of Ye et al. (1992), and subsequently by treating them as missing data in the outgroup.

Our analysis using the polarizations of Ye et al. (1992) for characters 7–11, 15, and 17 resulted in 16 MPTs, 60 steps in length (ci = 0.45, ri = 0.53). The strict consensus tree is identical to that of the original analysis with only three nodes resolved. Using successive weighting resulted in a single MPT which is one of the 16 MPTs (Fig. 4). When supporting characters were mapped on the phylogeny, most of the nodes received very little unambiguous support from these data.

The alternative approach treated character states that were unknown in the outgroup as missing data. This resulted in 1 most parsimonious tree (Fig. 5), ci =

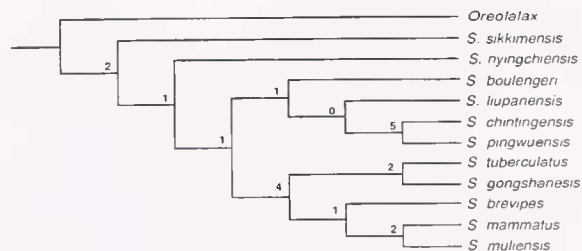


Figure 5. A single MPT for the relationships of *Scutigera*. The data in which unknown states for the outgroup are left as missing. Numbers indicate unambiguous synapomorphies occurring at each node.

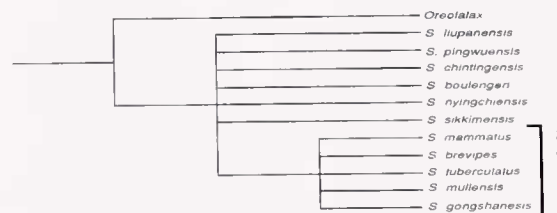


Figure 6. The resulting strict consensus tree of *Scutigera* after saving all trees one step longer than the shortest tree, from the data set where unknown outgroup states were left as missing.

0.49, $ri = 0.57$ and 59 steps. In this topology, like the others, few unambiguous changes have occurred.

Discussion

Ye et al. (1992), recognized two subgenera in the genus *Scutigera*: *Scutigera* and *Aeluophryne*. They identified three synapomorphies for the latter, and based on the derived relationships and current distributions, drew conclusions about the origin of the scutigerae.

Our results show that the phylogeny of Ye et al. (1992) was not the most parsimonious explanation of their data. We resolved 20 trees that were more parsimonious. A strict consensus of our shortest trees resulted in a tree with only three nodes resolved. As was true in Ye et al.'s tree, *Aeluophryne* was monophyletic and supported by three synapomorphies. Within this clade the sister relationships of only two species, *S. tuberculatus* and *S. gongshanensis*, could be unambiguously resolved. The remaining scutigerae formed a single basal polytomy with the *Aeluophryne*, but two species were resolved, *S. chintingensis* and *S. pingwuensis*. This sister relationship was also seen in Ye et al.'s tree. Our analysis did not resolve the subgenus *Scutigera* as a monophyletic group.

Ye et al. (1992) apparently used a hypothetical ancestor rather than *Oreolalax* as the outgroup, some characters were incorrectly polarized. Consequently, we believe that any conclusions derived from either their phylogeny or our reanalysis of the original data set are invalid.

The proper ordering and polarizations of character states using the outgroup criterion proved very important. Failure to defensibly order states of multistate characters resulted in the resolution of less parsimonious solutions. Even though we changed the polarizations of two characters, seven other characters could not be polarized. Consequently, subsequent analyses either left the polarization as assumed by Ye et al

(1992), or we treated the outgroup states as missing, thereby treating the characters as unpolarized. The former analysis resulted in 16 MPTs in which the strict consensus tree was identical to our first analysis. The latter analysis resulted in one tree depicting *Aeluophryne* as monophyletic, and *S. chintingensis* and *S. pingwuensis* as sister species. It did not resolve the subgenus *Scutigera* as a monophyletic assemblage.

It is desirable to assess the support for individual nodes and the entire phylogeny. Several methods have been proposed. One procedure, bootstrap (BS) analysis (Felsenstein, 1985), assesses relative support for each node of a phylogeny (for criticisms of the method see Carpenter, 1992; Hillis and Bull, 1993; Kluge and Wolf, 1993; Trueman, 1993). One prerequisite to a BS analysis often overlooked, is that a minimum three characters per node is required to obtain a statistically significant BS value. Unfortunately, our MPTs do not have enough unambiguous character changes at each node to generate statistically meaningful BS values.

Decay analysis (Bremer, 1988), an alternative method, keeps all trees that are a specified length longer than the MPTs. It permits the assessment of nodal support by identifying only those monophyletic groups that are common to all of the possible trees. This method presumes that all relationships receiving sound support from these data will be present in a strict consensus tree of all trees one or two steps longer. When we held all MPT plus those one step longer, 241 trees were retained. The resulting strict consensus tree showed no resolution; all of the ingroup taxa were resolved from a single node. However, when the ambiguously polarized states were coded as missing data in the outgroup, the MPTs and those one step longer included 27 trees, and the strict consensus tree broke into one ingroup clade, *Aeluophryne* (Fig. 6). Holding all trees two steps longer resulted in 362 trees and a single polytomy.

The status of the subgenera *Aelurophryne* and *Scutigera* has been debated (Myers and Leviton, 1962; Noble, 1931; Pope and Boring, 1940; Liu, 1950) and *Aelurophryne* was previously diagnosed by the absence of maxillary teeth. Meyers and Leviton (1962) stated that the absence of teeth actually reflected a graded trend within the genus *Scutigera*, and could not be used to separate *Scutigera* from *Aelurophryne*. This is also true for two of the three characters used by Ye et al. (1992) to define *Aelurophryne*. However, the presence of a robust metacarpal bone can be used to distinguish *Aelurophryne* from other scutigers.

Ye et al. (1992), used their phylogeny to discuss the evolution and specialization of *Aelurophryne*. They described the subgenus as having become more specialized for an aquatic lifestyle, and recognize three synapomorphies: robust metacarpal bone, thick humerus, and the no keritanized spines on the dorsum. Two problems exist. First, the latter two synapomorphies are also derived in *S. nyingchiensis*. Second, one synapomorphy, no keritanized spines, is an actual loss of a character. It is more preferable when reconstructing phylogenies to use characters that are uniquely derived and not represented by the absence of characters. Moreover, characterizing a group based on the absence of traits should be avoided. Numerous scenarios can be developed to explain the loss of a character and its homologue can never be identified with certainty. However, the presence of a character may be scrutinized at a greater detail, often making it possible to recognize homologous counterparts.

Because the subgenus *Scutigera* cannot be diagnosed, it is possible, if not likely that this subgenus is a polyphyletic assemblage of species. Therefore, our analysis requires that the subgenus *Aelurophryne* not be recognized if a holophyletic classification is to be maintained.

One problem that permeates the data base is the selection of highly homoplastic characters. Homoplastic characters tend to provide no definitive resolution. However, we cannot comment on the quality of characters until we can see how they perform during a defensible phyletic estimation. We are certain that too few characters were used to generate support for any of the relationships on the phylogeny.

The information summarized by Ye et al. (1992) forms the initial ground work for understanding the evolutionary relationships *Scutigera*. Given that so little is known about these frogs, any advances should be deemed valuable. However, additional data are required to confidently resolve the phyletic relationships of scutigers, and to identify the corresponding

plesiomorphic condition in *Oreolalax*. Once a sound phylogeny of the genus has been achieved, it will be possible to address biogeographical, ecological, and behavioral questions.

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Appendix I

Modified data set of Ye et al (1992). Characters were polarized using *Oreolalax* as the outgroup. Those characters in bold were omitted from the analysis because they are apomorphic.

Character	1	111111	111112	22222	2222	
number	12345	67890	12345	67890	12345	6789
<i>Oreolalax</i>	00100	00000	00000	00000	0000-	0100
<i>S. liupanensis</i>	11101	00011	10101	01101	11010	0000
<i>S. pingwuensis</i>	01111	00111	10001	00101	11011	0011
<i>S. chintingensis</i>	00111	01101	00001	01001	11001	0011
<i>S. boulengeri</i>	01101	10000	10100	01100	11010	0000
<i>S. nyingchiensis</i>	01001	00001	01000	11011	10000	0001
<i>S. sikkimensis</i>	01100	11111	00000	01111	11000	1001
<i>S. mammatus</i>	01001	10010	01110	10100	10100	0001
<i>S. brevipes</i>	01101	10000	01110	10101	10000	0001
<i>S. tuberculatus</i>	01011	10000	01110	11101	10000	0011
<i>S. muliensis</i>	01011	10000	01110	10101	10100	0001
<i>S. gongshanensis</i>	00111	10011	11110	11110	00000	0111

Appendix II

Character used by Ye et al (1992).

1. Head width to length
0: width > length, 1: width < length
2. Maxillary teeth
0: well developed, 1: very small or absent
3. Nasal and sphenethmoid
0: articulated, 1: seperated
4. Columella
0: present 1: absent
5. Quadratojugal
0: long, articulated or overlapped with maxilla,
1: short, wildy seperated from maxilla
6. Prootic and exoccipital bone
0: seperated. 1: fused
7. Hyoid plate plus anterior process (HPAP) and the distance between the out flank of the anterior process (DFAP)
0: HPAP < DFAP, 1: HPAP > DFAP
8. Hyoid fenestra
0: present 1: absent
9. Cricoid cartilage
0: complete circle, 1: circle incomplete
10. Omosternum and xiphisternum
0: Width of omosternum < width of xiphisternum, 1: width of episternum > width of xiphisternum
11. Omosternum
0: partially ossified, 1: entirely cartilage
12. Humerus in male
0: length/width > 4, 1: length/width < 4
13. Inner crest of radioulna in male
0: absent, 1: present
14. Inner two metacarpals and phalanges in male
0: normal, 1: robust
15. Prepollex
0: ossified, 1: cartilage
16. Dorsal skin
0: with horny spines, 1: without horny spines
17. Large warts near vent
0: absent, 1: present
18. Post-femoral gland
0: present, 1: absent
19. Webbing between toes
0: present, 1: absent
20. Metatarsal tubercle
0: absent, 1: present
21. Vocal sac
0: present, 1: absent
22. Spiney patches on the chest
0: one pair, 1: two pair
23. Spines on the chest
0: small, 1: big
24. Spinal warts on belly
0: absent, 1: present
25. Spinal patches of forelimb
0: absent, 1: present
26. Nuptial spines
0: small, 1: big
27. Linea musculinae
0: absent, 1: present
28. Labial margin of tadpole
0: narrow, with many tubercles, 1: wide, with few or no tubercles
29. Labial teeth formula of tadpole. Number of tooth rows
0: $\geq 1:5-5/I:5-5$, 1: $< 1:5-5/I:5-5$.